

**An illustrated key to the species of *Grania* and *Randidrilus*
(Annelida: Clitellata: Enchytraeidae) of eastern North America,
Bermuda, and the Caribbean area**

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Abstract.—The marine, clitellate genus *Grania* Southern, 1913 is a globally prevalent group of enchytraeids in intertidal and shallow subtidal habitats, showing high diversity in tropical and subtropical latitudes. Due to the rapidly rising numbers of known species of *Grania*, taxonomic revisions, and modifications in species ranges, a basic aid to species recognition is required for systematic, biodiversity, and ecological studies. A dichotomous key using anatomical characters distinguishes the nine species of *Grania* and two species of the co-occurring and structurally similar genus *Randidrilus* Coates & Erséus, 1985, with known distributions within eastern North America, the neighboring islands of Bermuda, and the Caribbean area. Based on examination of type and recent material, annotations on structural details of the male ducts and statocysts of each of the nine *Grania* species are provided.

Grania of the Northwest Atlantic

The coastal habitats of eastern North America, the Atlantic islands of Bermuda, and the Caribbean area have not been extensively surveyed for marine enchytraeid clitellates and new species are regularly found in unsuspected habitats (Healy 1994, Healy & Walters 1994, Healy & Coates 1999). In some of the few taxonomic surveys, the genus *Grania* Southern, 1913 (Enchytraeidae) was relatively diverse or abundant (Kennedy 1966, Lasserre 1971, Erséus & Lasserre 1976, Lasserre & Erséus 1976, Coates & Erséus 1985) (Fig. 1). Based on existing but undescribed collections, the range of unexplored locations and microhabitats, and investigation of new structural and genetic characters, it is expected that a number of new species remain to be discovered in this geographic region. Readily available and accessible information about known species is essential to the recogni-

tion of new species, and ensuing studies of the diversity of *Grania*.

Species of *Grania* are infaunal, sometimes interstitial, indistinctly segmented worms. They are found in well-sorted medium to coarse sand as well as poorly sorted sandy-mud, both intertidally and in the shallow subtidal. Deep water species are found in clay, silt, and sandy-silt. Sexually mature worms range from about 3–15 mm long and from about 0.08–0.25 mm in diameter. Specimens of *Grania* are distinguished from other marine enchytraeids by their robust, straight, pointed setae which occur singly both ventrally and laterally. These setae are lacking completely in at least one species, *Grania levis* Coates & Erséus, 1985. The unpigmented body wall is relatively rigid due to a thick cuticle, causing the worms movements to be stiff and sigmoid, like those of a nematode. The key characteristics for distinguishing species of *Grania* are the shape and distribution of setae, shape of spermathecae, and structure of

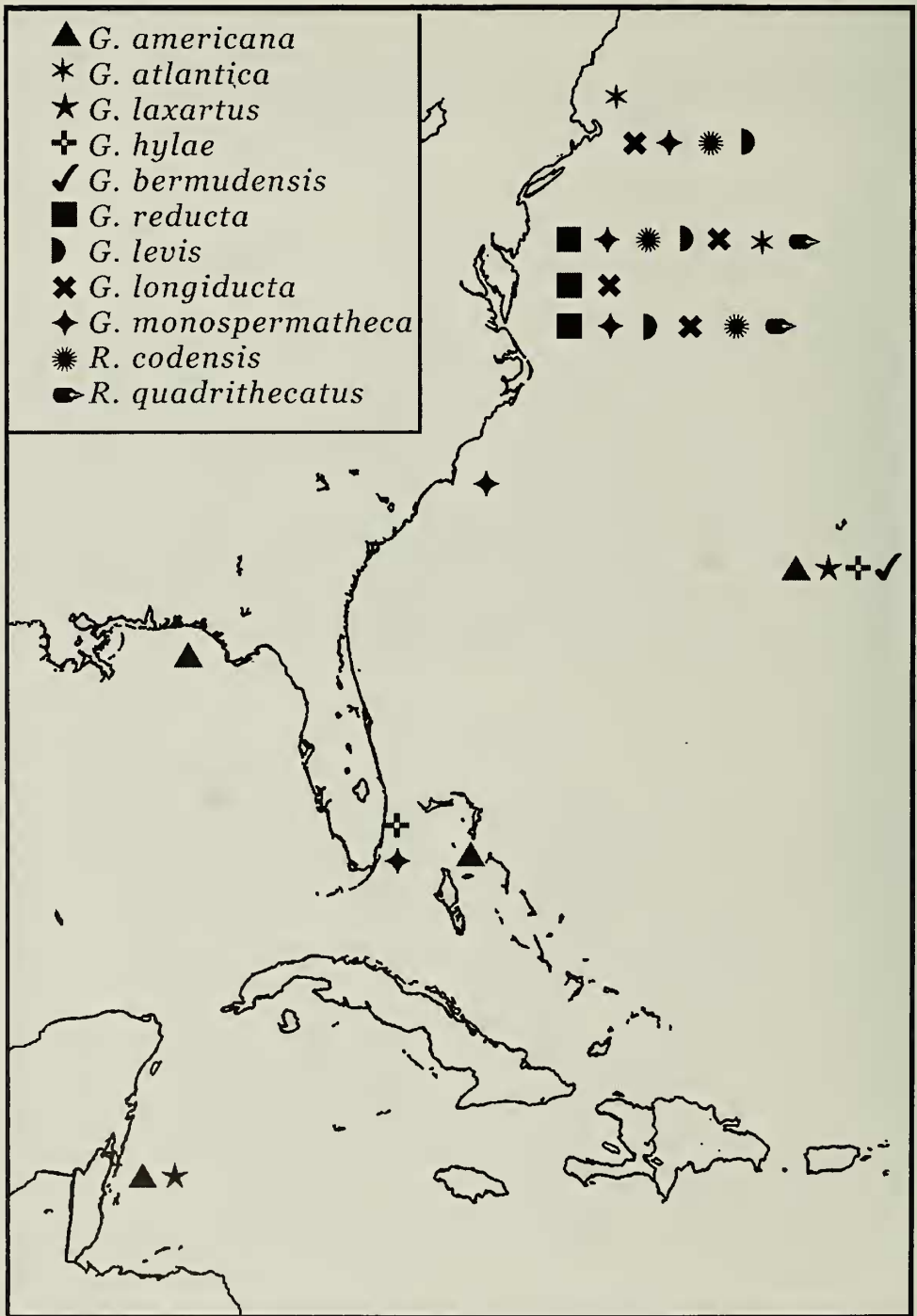


Fig. 1. Known locations of *Grania* species in the Western Atlantic and Caribbean.

the male duct system—the sperm funnel, vas deferens, and penial apparatus (Fig. 2). Specimens must be mature to be identified to species. Nielsen & Christensen (1959) considered any enchytraeid specimens without a clitellum as immature and their reproductive structures incompletely formed.

Grania americana Kennedy, 1966, was the first enchytraeid recorded in a continental shelf habitat of Atlantic North America (Kennedy 1966, Coates & Erséus 1985, Locke & Coates 1999). A few years later, Lasserre (1971), working at the Marine Biological Laboratories of Woods Hole, Massachusetts, recorded three subtidal enchytraeid species, one of which he identified as *Hemigrania postclitellochaeta* (Knöllner, 1935). The genus *Hemigrania* Lasserre, 1971 has since been synonymized with *Grania* (Erséus & Lasserre 1976) and *Grania postclitellochaeta* does not occur in North American waters (see Coates & Erséus 1985). The material reported by Lasserre (1971) has been referred to *Grania longiducta* Lasserre & Erséus, 1976 (Coates & Erséus 1985). The area of Woods Hole remains the northern limit for records of *Grania* in eastern North America. Erséus & Lasserre (1976) made additions to the western North Atlantic fauna with records of *Grania monospermatheca* Erséus & Lasserre, 1976, from Cape Cod, Massachusetts, and *Grania bermudensis* Lasserre & Erséus, 1976 (see also Locke & Coates 1999) from the sub-tropical islands of Bermuda. Coates & Erséus (1985) described three new species, *Grania reducta* and *Grania levis*, from coastal eastern North America and *Grania atlantica* from deep Atlantic waters including the North American continental shelf. The most recently described species in the western Atlantic are *Grania laxartus* Locke & Coates, 1999 and *Grania hylae* Locke & Coates, 1999 from eastern Florida, Bermuda, and the Caribbean area.

Keys to North American Marine Enchytraeids

Cook & Brinkhurst (1973) prepared an annotated key for the northeastern United

States in which they presented information in standard couplet format for four families of “oligochaetes”, Enchytraeidae, Naididae, Tubificidae, and Megascolecidae (=Acanthodrilidae in Cook & Brinkhurst 1973). *Grania* was represented in the key by a single species, *Hemigrania postclitellochaeta*. As noted above, the taxonomic status of the specimens found in North America and originally called *H. postclitellochaeta* has since been amended (Coates & Erséus 1985). Although a number of *Grania* species are now recognized from the northwestern Atlantic (Coates & Erséus 1985, Locke & Coates 1999), a modern, comprehensive key does not exist for these species or for any other marine enchytraeids (Milligan 1996). In fact, enchytraeids have been excluded from all keys to aquatic oligochaetes of North America (see Brinkhurst 1986, Kathman & Brinkhurst 1998), and from regional keys (Strayer 1990; Milligan 1996, 1997).

The following key includes nine species of *Grania* recorded from the eastern coast of North America, Bermuda and the Caribbean area. Species of the enchytraeid genus *Randidrilus* Coates & Erséus, 1985, described from the North American coast by Coates & Erséus (1985), are quite similar to *Grania* in morphology and distribution. Due to their occurrence in the same habitats as some eastern North American *Grania* species, the two *Randidrilus* species from the region are included in the key presented here. Species identifications should be confirmed by reference to recent species descriptions (Coates & Erséus 1985, Locke & Coates 1999). Species included within the key are: *Grania americana*, *Grania longiducta*, *Grania atlantica*, *Grania monospermatheca*, *Grania bermudensis*, *Grania reducta*, *Grania hylae*, *Grania laxartus*, *Grania levis*, *Randidrilus codensis* (Lasserre, 1971) and *Randidrilus quadrithecatus* (Coates & Erséus 1985).

Materials and Methods

Whole-mounted specimens of *Grania* and *Randidrilus* were examined by light

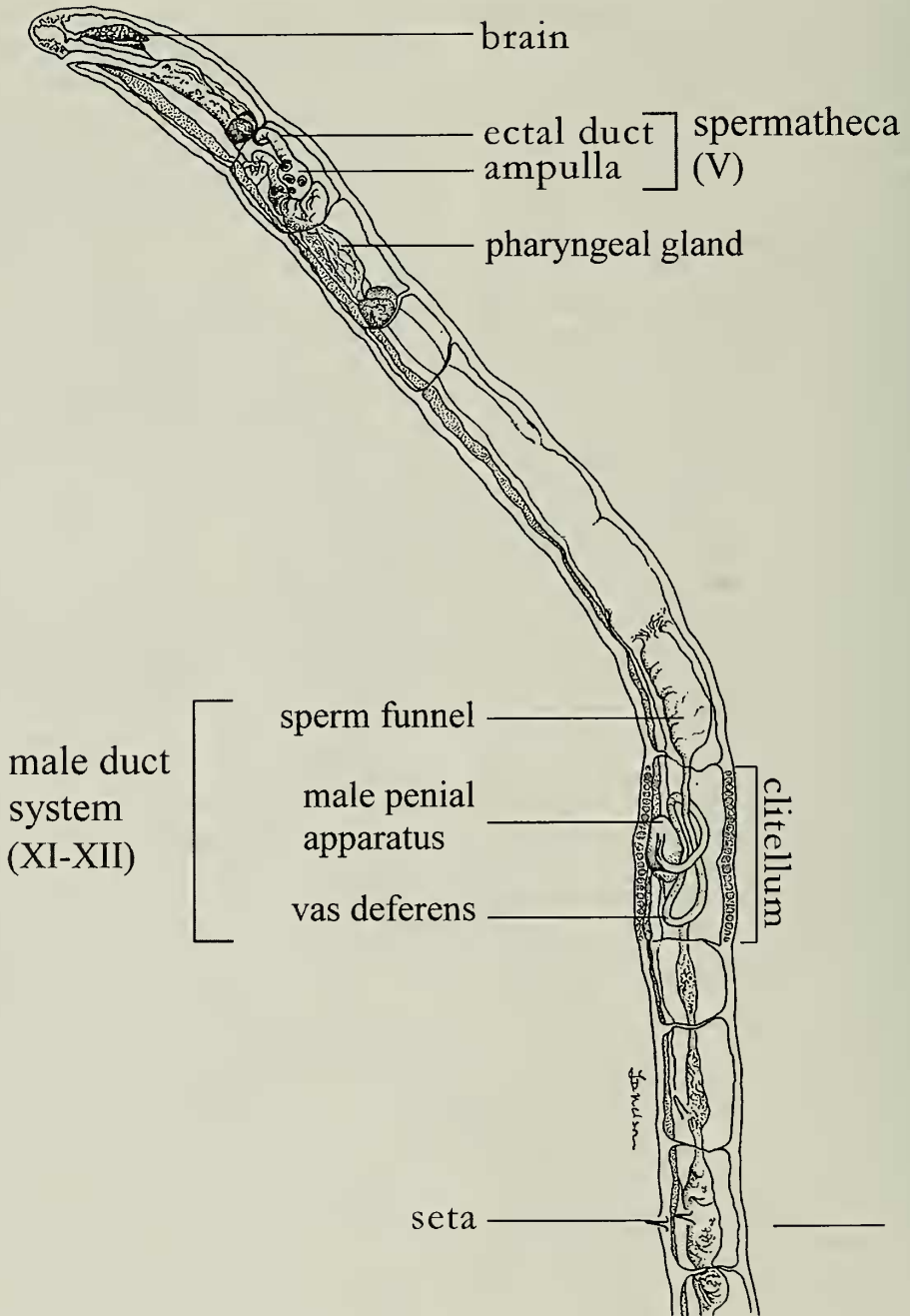


Fig. 2. General morphology of *Grania* species, based on *Grania longiducta*, illustrating main diagnostic characters. Scale equals 100 μ m.

microscopy to confirm characteristics for species included in the key. These included type specimens of *G. americana* USNM 33005, *G. bermudensis* USNM 53202, *G. hylae* USNM 185954, *G. levis* USNM 96509, *G. laxartus* USNM 185951, and *R. quadrithecatus* USNM 96498, from the United States National Museum of Natural History (USNM) (Smithsonian Institution), Washington, D.C. Other material of *R. codensis* ROMIZ 12177 (5 specimens) was borrowed from the Royal Ontario Museum (ROM), Toronto, Ontario, Canada. Specimens of other North American species of *Grania* were from the collections of C. Erséus and K. A. Coates (Locke & Coates 1999).

To separate higher taxa and to identify species, diagnostic characters were determined and definitions for these relevant to the enchytraeids developed (Appendix 1). Primary references for definitions were Nielsen & Christensen (1959), Stachowitsch (1992), Abercrombie et al. (1992) and Webster's Encyclopedic Unabridged Dictionary (1989).

An illustrated key to the species of *Grania* of eastern North America, Bermuda, and the Caribbean area also was developed as a website entitled, "Key to *Grania* of North America, Bermuda, and the Caribbean area." The World Wide Web Universal Resource Locator (URL) address for this website is: <http://www.bbsr.edu/users/kcoates/Grania/Grania.html>. This site is regularly maintained and updated.

Distinctive Characteristics of the Marine Enchytraeid Genera

Enchytraeids (Clitellata) are characterized morphologically by position and form of reproductive structures (Fig. 2) and by their setal shapes. When present, setae are straight, sigmoid or bent, rarely possessing a nodulus and rarely forked at the distal tip. No marine enchytraeids are known with forked setae. Spermathecae are anterior in segment V and rarely in VI. Testes are

Table 1.—Distinguishing characteristics for enchytraeid genera with marine species.

Genus	Distinguishing characters
<i>Achaeta</i>	lack setae head pore at tip of prostomium
<i>Enchytraeus</i>	unbranched peptonephridia
<i>Lumbricillus</i>	lobed testis sacs (except <i>L. semifuscus</i>)
<i>Marionina</i>	dorsal blood vessel bifurcation posterior to brain (few exceptions in marine species, e.g., <i>M. charlottensis</i>)
<i>Stephensoniella</i>	large compact pharyngeal glands thickened septa globose spermathecal diverticulum
<i>Randidrilus</i>	anterior and posterior glands at penial pore
<i>Grania</i>	stout, single setae (rarely absent) complex penial apparatus penial stylet may be present

paired in XI and ovaries are paired in XII. The pores of the male penial apparatuses are in segment XII and paired, glandular, pre-septal sperm funnels originate in XI, often extending or displaced into segments anterior and posterior to XI by body movements and contractions. There are seven genera (Healy & Coates 1999) known to have species in marine habitats, in contrast to about 22 terrestrial and freshwater genera. These genera are: *Achaeta* Vejdovský, 1878, *Enchytraeus* Henle, 1837, *Lumbricillus* Ørsted, 1844, *Stephensoniella* Cernovitov, 1934a (amended by Coates 1983), *Marionina* Michaelsen, 1889, *Grania* Southern, 1913, and *Randidrilus* Coates & Erséus, 1985. All of these have been recorded from the coastlines and continental shelves of eastern North America.

Combinations of a few characters can be used to distinguish among the marine enchytraeid genera. One or two species are atypical of their genus and may lack some otherwise distinguishing characteristics (Table 1).

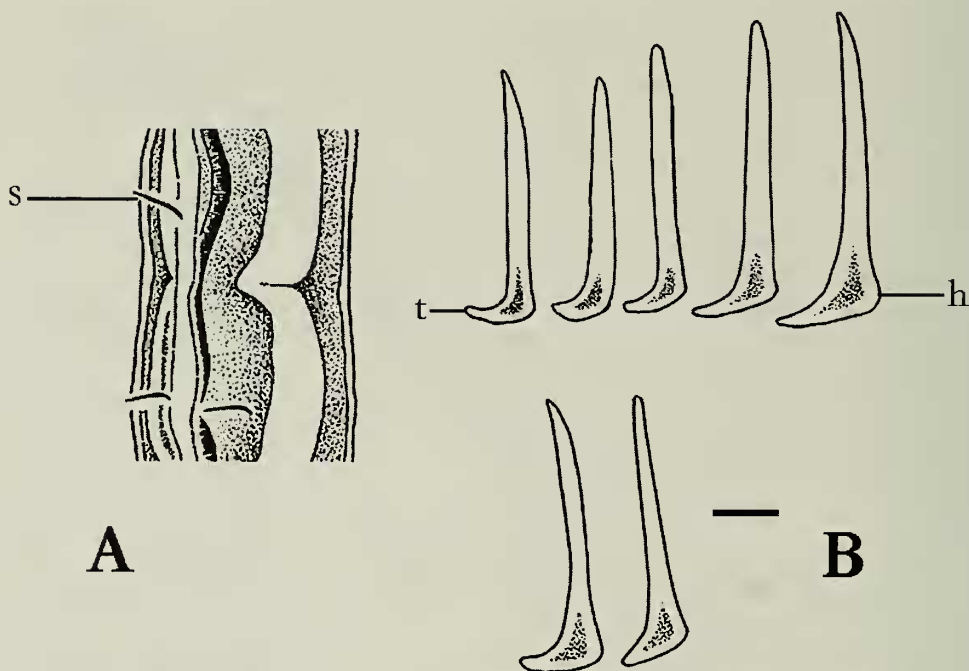


Fig. 3. Setae of *Grania*. A. Position of ventral setae in worm body. B. Setae, illustrating heel and toe characteristic of some species. Scale equals 20 μ m for B only. h, heel; s, seta; t, toe.

Specific terms or phrases in the following text are further explained in Appendix 1. The reproductive and nephridial systems mentioned for each of the following genera are paired systems, unless noted otherwise.

Species of *Achaeta* totally lack setae and may have one, two or three pairs of epidermal glands in each segment, called epidermal gland sacs; these sacs are lacking in the single marine species, *Achaeta littoralis* Lasserre, 1968. Spermathecae are in V or extend posteriorly as far as X; the ampullae are without ental ducts or other connections to the esophagus; the brain is convex posteriorly; the sperm sac is small and compact; the penial apparatus includes several small glands around the male pore. The head pore of species of *Achaeta* is near the tip of the prostomium.

Species of *Enchytraeus* possess paired, unbranched post-pharyngeal or esophageal appendages (see Schmelz & Westheide 2000); setae are straight with two or more in a bundle; glands are present at the spermathecal ectal pores; the brain is convex

posteriorly and each penial apparatus has either a single compact gland or a longitudinal row of glands along the ventral body wall.

Species of *Lumbricillus* have a lobed testis sac; setae are usually sigmoid, more than two per bundle; glands are present at the spermathecal ectal pore; the brain is incised posteriorly.

Species of *Marionina* may lack, or have straight or sigmoid, setae, which are single, paired or multiple per segment; spermathecae may have glands along the spermathecal ectal duct and/or at the spermathecal ectal pore; many marine species also have sperm rings, sometimes in distinct diverticula of the ampulla; the brain is incised or convex posteriorly; in each nephridium the nephridial canal extends anterior to the septum; the anterior dorsal blood vessel bifurcation in most species is posterior to the brain with circumpharyngeal vessels looping anteriorly, lateral to the brain (Coates & Ellis 1981, also see Coats 1980).

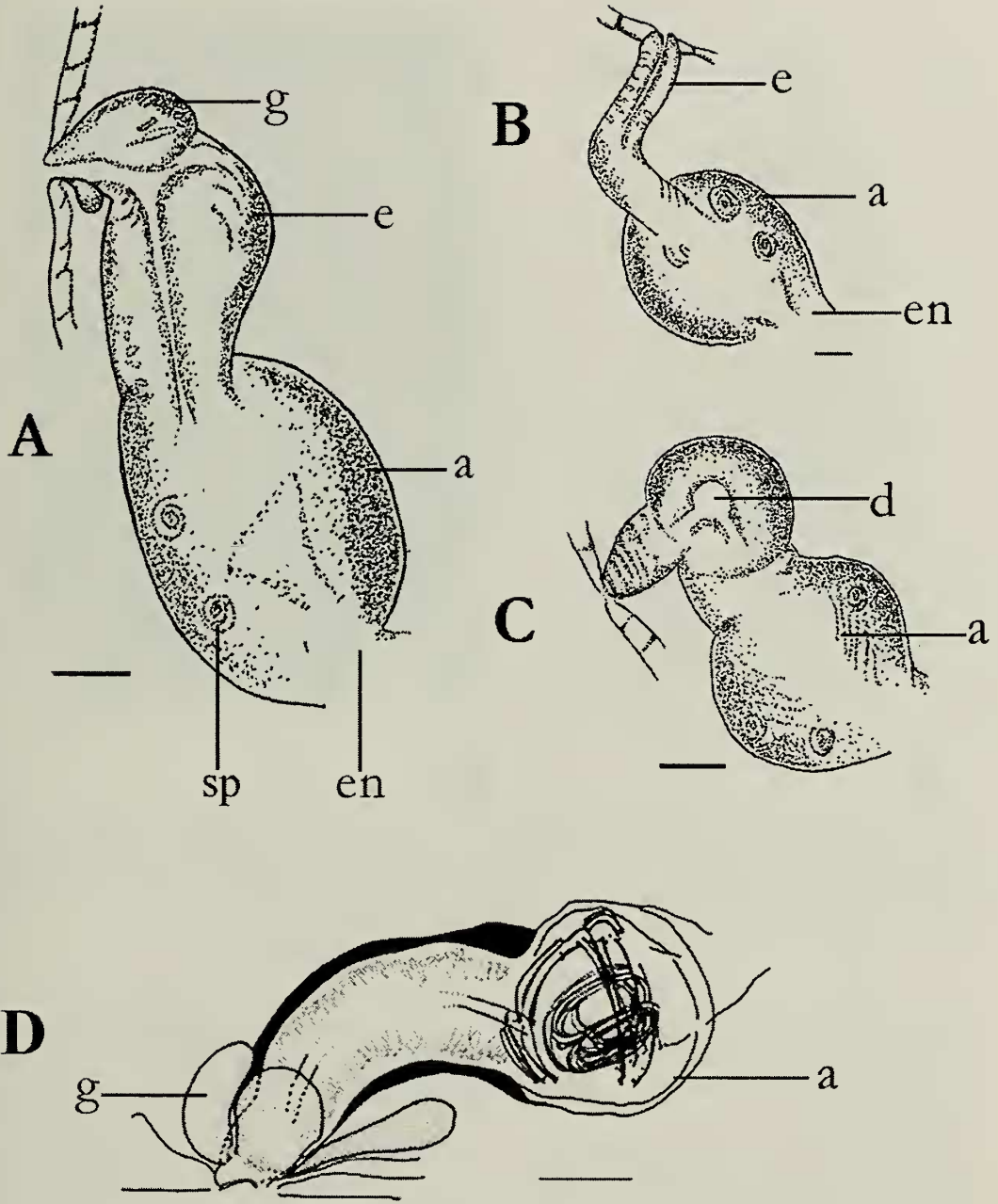
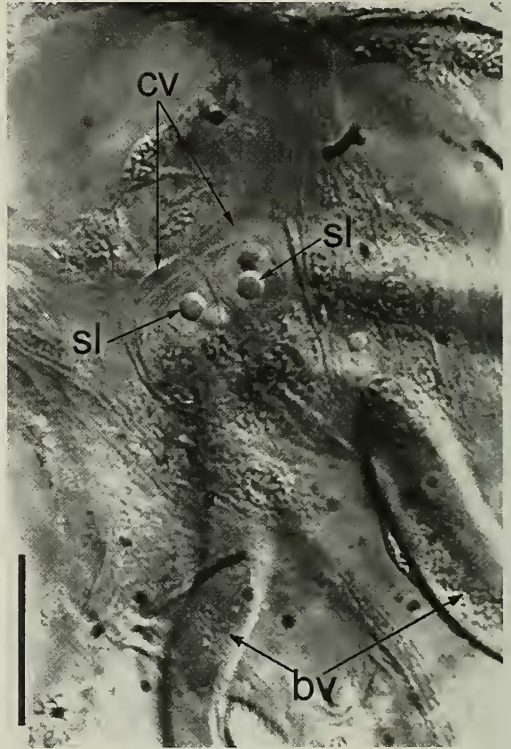
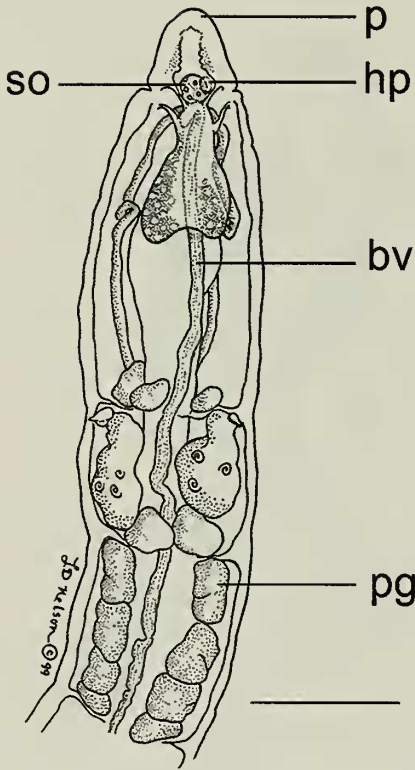


Fig. 4. Spermathecae. A. *Grania americana* with glands at ectal pore; B. *Grania hylae* with narrow ectal duct; C. *Grania laxarta* with distinct dilation of ectal duct; D. *Randirilus codensis* with glands at ectal pore. Scales equal 20 μ m. a, ampulla; d, ectal duct dilation; e, ectal duct; en, ental duct; g, gland; sp, sperm ring.

Stephensoniella species have bundles of only two or three slightly sigmoid setae; single compact penial glands; large compact pharyngeal glands and thickened mus-

cular septa from 5/6 to about 8/9; and each spermatheca has a globose or saccate ampullar diverticulum.

Randirilus species have single, ventro-



A

B

Fig. 5. *Grania americana*. A. Schematic illustration of whole mount showing anterior position of statocyst within the prostomial region. The bifurcation of the dorsal blood vessel is posterior to the statocyst which lies below the head pore. Scale equals 100 μ m. B. Chambered statocyst anterior to blood vessel bifurcation. Three of four statoliths are clearly shown. Scale equals 20 μ m. bv, dorsal blood vessel; cv, chambered statocyst; hp, head pore; p, prostomium; pg, pharyngeal gland; sl, statolith; so, statocyst.

lateral setae present as far forward as II; one or two pairs of spermathecae; and penial apparatuses with separate, compact, anterior and posterior glandular masses at each male pore.

Grania species have stout, single setae (Figs. 2 & 3), but setae lacking from at least some anterior segments; sperm rings in the spermathecal ampulla (Fig. 4); elongate, posteriorly extending sperm and egg sacs; and a diversity of complex penial apparatuses, sometimes with penial stylets.

Key for *Grania* and *Randidrilus*

The following dichotomous key should be used after determining the genus of the

specimens using Table 1 and the information given above. Observation of the characters used in the key requires a compound microscope and sexually mature specimens. Either live specimens or dehydrated, cleared, stained, and mounted specimens can be used (Locke 1999). Major characteristics used in the key are described in Appendix 1.

The hierarchy of the following key is wholly artificial. The numbers in parentheses indicate the couplet from which the current couplet was reached.

- 1. A. Ventral setae occurring anterior to clitellum 2

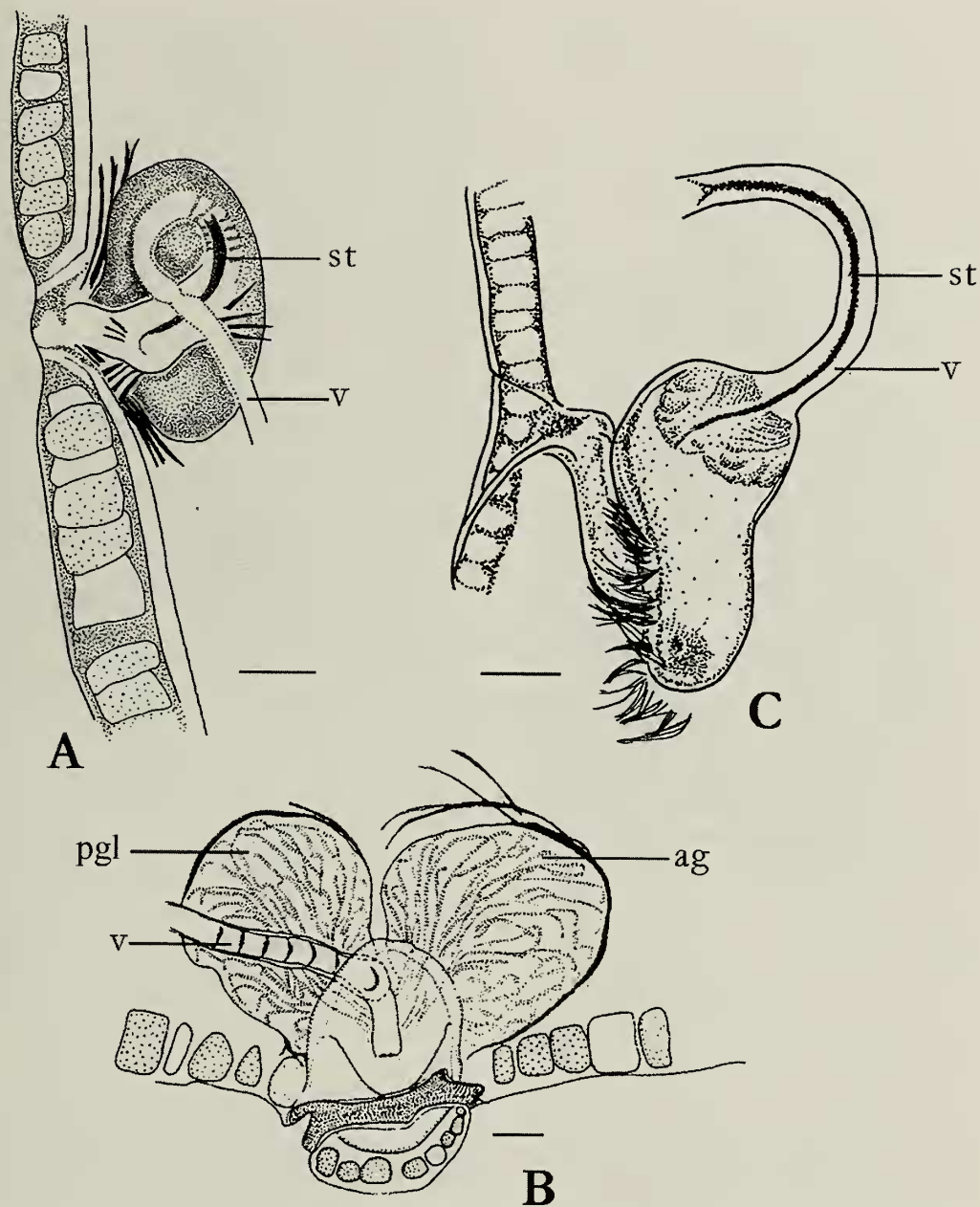


Fig. 6. Male penial apparatuses A. Bulbous gland of *Grania laxarta*, B. Whole apparatus of *Randidrilus codensis*, and C. Bipartite sac of *Grania bermudensis*. Scales equal 20 μ m. ag, anterior gland; pgl, posterior gland; st, stylet; v, vas deferens.

- | | | | | | |
|-----|---------------------------------------------------------------------|---|-----|------------------------------------------------------------|-------------------------|
| 2. | A. No ectal glands present at spermathecal pore | 5 | 3. | A. Statocyst present (Fig. 5) | |
| (1) | B. Ectal glands present at spermathecal pore (Fig. 4A, D) | 3 | (2) | Penial apparatus with single bulbous gland (Figs. 6A & 7B) | |
| | | | | Penial stylet absent | <i>Grania americana</i> |
| | | | | B. Statocyst not present | |

Penial apparatus with anterior and posterior glands at male pore (Fig. 6B)

Penial stylet absent 4

4. A. Two pairs of spermathecae present in V and VI

(3) Ventral seta in II, absent in III to XXI-XXVII

Lateral setae absent
 *Randidrilus quadrithecatus*

B. One pair of spermathecae (Fig. 4D) in V

Ventral setae from II

Lateral setae absent
 *Randidrilus codensis*

5. A. Spermathecal ectal pores dorsal

(2) Penial apparatus a bipartite sac, stylet present (Figs. 6C & 7A) 6

B. Spermathecal ectal pores lateral

Penial apparatus bulbous, stylet absent 10

6. A. Elongate muscular modifications of vas deferens (Fig. 7A)

(5) No statocyst anterior to brain
 *Grania bermudensis*

B. Muscular constrictions of vas deferens

Statocyst anterior to brain
 *Grania hylae*

7. A. Lateral, paired spermathecal pores

(1) Penial apparatus bulbous (Fig. 6A) 8

B. Mid-dorsal, single spermathecal pore

Penial apparatus a bipartite sac
 *Grania monospermatheca*

8. A. Penial stylet absent *Grania reducta*

(7) B. Penial stylet present (Fig. 6A & C) 9

9. A. Setae lacking entirely . . *Grania levis*

(8) B. Setae only postclitellar
 *Grania longiducta*

10. A. Bipartite spermathecal ectal duct

(5) Statocyst present . . *Grania atlantica*

B. Distinct dilation midway along spermathecal ectal duct (Fig. 4C)

Statocyst absent . . . *Grania laxartus*

Systematic Comments

Following are comments on the species included in the key. Particular attention has been given to new taxonomic structures and

our observations are noted as additional comments. Synonymies are found in the most recent references.

Grania americana Kennedy, 1966. Type locality: 0.5 km from North Entrance point, west side of North Bimini, Bahamas. Also known from Florida, Bermuda, and Carrie Bow Cay, Belize. Intertidal and shallow subtidal to 10 m, in sand and sandy-mud. Completely redescribed in Locke & Coates (1999).

Grania atlantica Coates & Erséus, 1985. Type locality: Continental slope off Massachusetts. Known from off the coast of New Jersey, SW of Ireland (NE Atlantic), N of Surinam, Guinea (W Africa) and Luanda, Angola. From depths of 744 to 1518 m, in silty-sand and ooze. Completely described in Coates & Erséus (1985), with new information in Rota & Erséus (1996).

Additional comments on the species: The anterior bilobed brain region consists of a thin extension which connects to an anterior statocyst (Locke 2000), referred to elsewhere as the "head organ" (Rota & Erséus 1996, Rota et al. 1999). The statocyst of *G. atlantica* differs from *G. americana* in that the statocyst vesicle is elongate rather than bulbous, the anterior medial extension of the brain is longer and three to four statoliths are apparent. The relative position of statoliths seem to differ from those of *G. americana* (see Locke & Coates 1999). A statocyst was only clearly visible in three of 21 preserved specimens of *G. atlantica*.

Grania bermudensis Lasserre & Erséus, 1976. Type locality: Castle Island, St. George's, Bermuda. Known only from Bermuda. Shallow subtidal, 8 to 15 m, in coarse coral sand with ripple marks. Completely redescribed in Locke & Coates (1999).

Grania hylae Locke & Coates, 1999. Type locality: ENE of Paget Island, St. George's Bermuda. Also known from Fowey Rocks, Florida. Intertidal, and subtidal, to 17 m, in medium to coarse coral sand, and muddy sand.

Grania laxartus Locke & Coates, 1999.

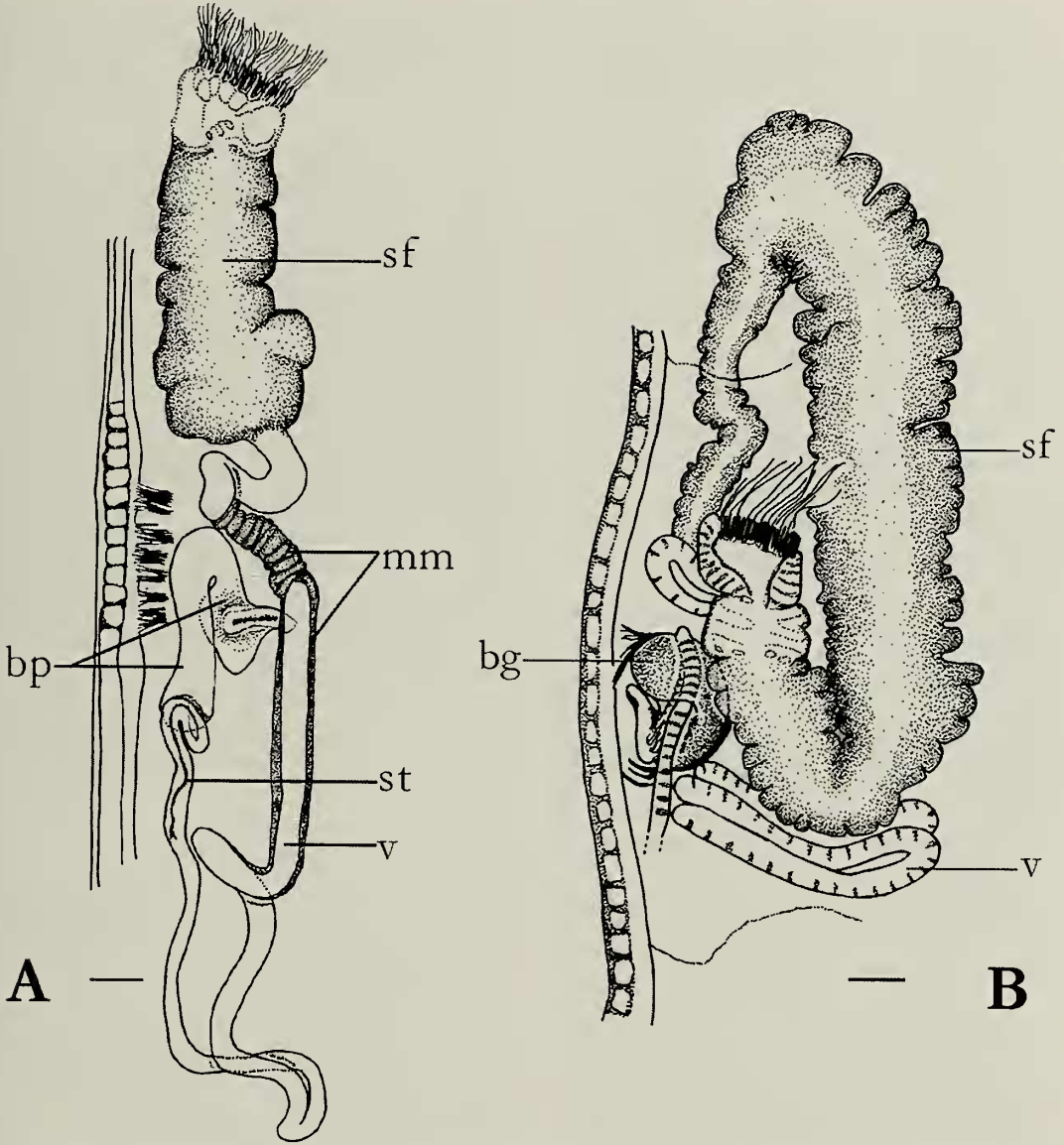


Fig. 7. Male duct systems of A. *Grania bermudensis* and B. *Grania americana*. Scales equal 20 μm . bp, bipartite sac; bg, bulbous gland; mm, muscular modifications; sf, sperm funnel; st, stylet; v, vas deferens.

Type locality: Ferry Point Bridge, St. George's, Bermuda. Also known from Carrie Bow Cay, Belize. Intertidal in poorly sorted coarse biogenic mud and sand.

Grania levis Coates & Erséus, 1985. Type locality: George's Bank (SE of Massachusetts). Also known from off the coast of New Jersey. Subtidal, 42 to 79 m, in medium to coarse sand.

Additional comments on the species: Statocyst not observed in holotype, which appears to be a typical specimen. Thus, it is unlikely that this species has this structure.

Grania longiducta Erséus & Lasserre, 1976. Type locality: Cape Cod Bay, Massachusetts. Also known from George's Bank (SE of Massachusetts), off the coast

of New Jersey, Delaware and Maryland. From depths of 42 to 78 m, in medium to coarse sand. Coates & Erséus (1985) made taxonomic revisions and annotations pertinent to this species.

Additional comments on the species: A narrow, possibly spiraled extension was visible within the anterior region of the bilobed brain; however, a statocyst was not seen anterior to this in 13 fixed and mounted specimens.

Grania monospermatheca Erséus & Lasserre, 1976. Type locality: Cape Cod Bay, Massachusetts. Also known from off the coast of New Jersey, Maryland, North Carolina, NE of Oregon Inlet, Beaufort, North Carolina, and Biscayne Bay, Florida. Subtidal, 3 to 48 m, in sandy-gravel. Redescribed in Coates & Erséus (1985).

Additional comments on the species: The penial apparatus is a terminal bipartite sac, it lacks a bulbous gland and contains a long stylet within a muscular, modified vas deferens. This is called a Type 6 penial apparatus (Coates 1984, Locke & Coates 1999). A statocyst was not seen in any of the 40 preserved specimens observed.

Grania reducta Coates & Erséus, 1985. Type locality: Off the coast of Maryland. Also known from Delaware, and off the coast of New Jersey. From depths of 29 to 65 m, in medium to coarse sand.

Additional comments on the species: Statocyst not observed in two preserved specimens from our collections.

Randidrilus codensis Coates & Erséus, 1985. Type locality: Cape Cod Bay, Massachusetts. Also known from off the coast of New Jersey and Maryland. From depths of 6.7 to 33 m, in medium to coarse sand.

Additional comments on the species: Statocyst not observed in the five preserved specimens that were available.

Randidrilus quadrithecatus Coates & Erséus, 1985. Type locality: off the coast of New Jersey. Also known from Maryland. From depths of 29 to 58 m, in medium to coarse sand.

Additional comments on the species:

Statocyst not seen in holotype, which appears to be a typical specimen. Thus, it is unlikely that this species has this structure.

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Appendix 1

Diagnostic characters and definitions for enchytraeids

ampulla (-ae): the ental, enlarged portion of the spermatheca (Figs. 2, 4). Sperm donated by a mate are stored in this part of the spermatheca prior to intracocoon egg fertilization. The ampulla is connected to the exterior of the worm by the ectal duct and an epidermal ectal pore. In species of *Grania* and of the other genera with marine taxa, except *Achaeta*, the ampulla is connected internally to the gut by the ental duct. In most species of *Grania* and some of *Marionina*, sperm rings form in the walls of the ampulla. The ampulla may itself have a single, or several, lateral outpocketings or diverticula.

bipartite penial sac: a complex sac at the terminus of the penial apparatus, in segment XII, found in species of *Grania*. It consists of two parts joined at a right or acute angle. The ectal or proximal part is an erect invagination of the male pore. The ental or distal part is a longitudinally oriented, muscular sac; when contracted, the walls of this part may be longitudinally ridged. A penial stylet extends into the ridged, ental sac (Figs. 6, 7). The term bipartite, saccate penial apparatus is used for the type of penial apparatus possessing such a sac, Type 6 (Coates 1984, amended by Locke & Coates 1999).

bulbous penial gland: a compact gland, associated with the male pore, in segment XII. Bulbous penial glands may lie alongside and open into an extended invagination of the male pore, or may lie dorsal to and open into a simple, epidermal, male pore. The gland is penetrated by the ectal part of the vas deferens. In species of *Grania*, a penial stylet may extend through the bulbous gland to an extended invagination of the male pore (Figs. 6, 7). In *Randidrilus* there is an anterior and a posterior bulbous gland (Fig. 6B).

clitellum: a region of enlarged, secretory, epidermal cells (see Jamieson 1981) extending from about XI-XIII (Fig. 2). The cocoon into which eggs are released is formed by secretions from the clitellum. In enchytraeids, the epidermal layer of the clitellum is just one cell thick; male (sperm) and female (egg) ducts and pores are within the region of the clitellum; no setae are present ventrally on segment XII once the clitellum is formed.

dorsal blood vessel bifurcation: anteriormost region of the dorsal blood vessel, where it divides to form two, lateral circumpharyngeal vessels (Fig. 5) which travel ventrally, then medially and posteriorly to unite as the ventral vessel. This bifurcation may lie posterior to the brain or near its anterior margin.

ectal duct: duct-like part of the spermatheca lying between the external spermathecal ectal pore and the ampulla (Figs. 2, 4). Sperm from a mate are transported through the ectal duct to the ampulla and, later, out to fertilize eggs. The ectal duct may have glandular cells along its length and/or at its junction with the

ectal pore. The ectal duct may have distinctive dilations or regionation of cell types.

ectal gland: unicellular or multicellular gland at the spermathecal ectal pore (Fig. 4); probably of epidermal origin.

ectal pore: opening of spermathecal ectal duct to the exterior (Fig. 4), located dorsally or ventrolaterally in furrow between segments IV and V, or just posterior to this on segment V and, rarely, VI (see *Randidrilus quadrithecatus*). Usually paired; a few species (e.g., *Grania monospermatheca*) have a single, middorsal pore.

ental duct: duct-like part of the spermatheca between the ampulla and the esophagus; an open canal to the esophagus may be present (Fig. 4). The specific function of an open connection is a matter of speculation (Locke 1999, p. 20; Westheide 1999). It could allow the flow of fluids and intestinal materials between the gut lumen and the spermatheca.

epidermal gland sac: found only in some species of *Achaeta*, all of which lack setae. The solitary sacs are laterally paired and there may be up to three pairs per segment. They are either dorsolateral, or dorso- and ventrolateral, or dorso-, medio- and ventrolateral. Nielsen & Christensen (1959) referred to these as setal follicles or gland sacs but noted that "their true nature is doubtful" (op. cit., p. 16). Setal follicles is synonymous with seta-producing sac or setal sac (Stachowitsch 1992) so the use of that name for the glandular sacs of *Achaeta* implies an homology which is not substantiated.

esophageal (see also oesophageal) appendage: tubular or bulbous organs extending from the posterior of the pharynx or anterior of the esophagus (see Schmelz & Westheide 2000); free floating in the coelom or lying on the dorsal surface of the gut. The unpaired forms are found in the genus *Achaeta*. According to Nielsen & Christensen (1959, 1963) "peptonephridia" are a particular form of these appendages, found only in species of *Enchytraeus*, *Enchylea* Nielsen & Christensen, 1963 and *Fridericia* Michaelsen, 1889. There is no evidence of an ontogenetic relation of these organs to nephridia which is implied by the name peptonephridia (Schmelz & Westheide 2000) and we recommend use of that name be discontinued. At one time there was confusion about the presence of "peptonephridia" in species of *Grania* and this led to the erection of the genus *Hemigrania* for *Grania*-like species which did not have "peptonephridia" (see Locke & Coates 1999). It is now clearly recognized that no species of *Grania* have esophageal appendages (Erséus & Lasserre 1976). The terrestrial genus *Hemienchytraeus* Cernosvitov, 1934b, has a basally unpaired post-pharyngeal or esophageal appendage which Nielsen & Christensen (1959) specifically do not call a peptonephridium. Coates (1987, 1989a, 1989b) studies indicate that this unpaired esophageal appendage had independent origins from the peptone-

phridia of species of *Fridericia* but detailed studies of these structures are in their infancy (Schmelz & Westheide 2000) and nothing is conclusive about their homologies.

head pore: unpaired, dorsal opening from body cavity to the exterior (Fig. 5). Located on the anterior part of the peristomium, at the junction of the peristomium and prostomium, or near the anterior tip of the prostomium as in *Achaeta* and a number of terrestrial enchytraeid genera.

lobed testis sac: lobed, peritoneal membrane enclosing testis, spermatocytes and sperm; originating ventrally on posterior face of septum between segments X and XI (septum 10/11) in the region of the testis. Individual lobes are drop- or pear-shaped. Found in species of *Lumbricillus*. There is one multi-lobed sac for each testis. Stephenson (1930), Coates (1987, 1989a) and Rota (1994) discussed differences between testis sacs and seminal vesicles or sperm sacs.

penial apparatus: the part of the male reproductive system located in segment XII, lying between the ectal end of the vas deferens and the external opening of the male reproductive system (Fig. 2). The penial apparatus of marine enchytraeids may have a penial stylet protruding from the vas deferens, a bipartite sac, a bulbous gland, and an epidermal infolding or invagination at the male pore (Figs. 6, 7). Gustavsson & Erséus (1997) provided a general discussion of atria and prostate glands of aquatic oligochaetes. In that paper, they refer to the penial apparatus of all enchytraeids as the penial bulb. Evolution from a simple male pore to a complex invagination and glandular apparatus at the male pore has occurred within the enchytraeid lineage (Coates 1987, 1989a) so that they do not have homologues of atria and prostates of, for example, tubificid oligochaetes. However, the terms atrium (or genital atrium) and prostate are applied to structurally and functionally comparable or analogous elements of the male reproductive systems of many lineages of animals (Abercrombie et al. 1992), including enchytraeids (Rota 1994). The complex forms of penial apparatus seen in species of *Grania* (Coates 1984, Locke & Coates 1999) were not known when the term penial bulb was first applied to the male pore apparatus of enchytraeids and does not adequately encompass these forms or the simplest forms of the penial apparatus (see Rota 1994).

penial stylet: slender, tapering, tube-like structure in the penial apparatus, reported for some *Grania* species; extends from ectal portion of vas deferens into bulbous penial gland or bipartite penial sac; possibly cuticular (Figs. 6A, C, 7A).

penial gland: a general term for a gland associated with the penial apparatus. In enchytraeids penial glands are usually located, with ducts opening, near or at the male pore. See comments on prostate under penial apparatus.

pharyngeal gland: compact glandular mass which

may occur on the septa at the posterior of segments from IV to VI, or VIII in some species of the freshwater *Cognettia* Nielsen & Christensen 1959, and ventrally in the same segments (Figs. 2 & 5A). Pharyngeal glands are laterally paired in each segment in which they are present. The compound extensions of these glands run ventrolaterally in a compact strand of tissue, anteriorly from the gland masses to the dorsal pharyngeal pad.

post-pharyngeal appendages: see esophageal appendages.

seta(e): also called chaeta(e); chitinous bristles which project from secretory setal sacs in the body wall (Figs. 2, 3); with special epidermal musculature allowing complex movements. Ectal tip single-pointed for all but one freshwater (*Barbidrilus* Loden & Locy, 1980) and one terrestrial (*Aspidodrilus* Baylis, 1914) genus of enchytraeid, variously shaped shaft. General distribution pattern is in four groups or bundles on each segment posterior to the peristomium and anterior to the pygidium. In enchytraeids, the setae are located in two ventrolateral bundles and two more or less lateral bundles on each segment. Setae are never found on the peristomium (i.e., body segment I of oligochaetes); some or all bundles may be missing from one to all other segments. Among marine species, espe-

cially *Grania*, *Randidrilus* and some species of *Marionina*, setae occur singly, rather than in bundles. Jamieson (1981) and Gustavsson (1999) discussed the structure and formation of oligochaete setae.

sperm ring: ring-like bundle of spermatozoa embedded in the walls of the spermathecal ampulla (Fig. 4A–C). Sperm rings are seen in species of *Grania* and marine species of *Marionina*. Mechanism and reason for their formation are unknown. Also see ampulla.

spermatheca(e): female reproductive structure which receives and stores sperm from a mate. Consists of two or three main parts: ectal duct and ampulla, and sometimes an ental duct (Fig. 4); ectal origin in V and, rarely, also in VI; may be paired or single in species of *Grania*.

statocyst: vesicular, ciliate organ with globular inclusions or statoliths (Fig. 5), located anterior to the brain (Rota et al. 1999, Locke 2000); thought to be a geotactic or equilibrium organ; reported only in species of *Grania*; lies below head pore and is dorsal to the anterior bifurcation of the dorsal blood vessel.

vas deferens (vasa deferentia): duct connecting sperm funnel to penial apparatus; with ciliated canal through which sperm travel to the male pore. In species of *Grania*, muscular modifications may be present as bandlike constrictions, knots (short spirals), elongate spirals, and longitudinal bands (Fig. 7).